DIFFERENTIAL RESPONSE TO FORM AND PATTERN IN TWO SPECIES OF INDIAN HONEYBEES[1]

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(With two text figures)

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1. Introduction

Honeybees are the most important among the social Hymenoptera as agents for pollination in plants. This is mainly due to their faculty of flower constancy, by which is meant the attachment of honeybees to flowers of a particular species of plant for obtaining nectar and pollen for a considerable period of time. In returning to the same type of flower and in being able to distinguish between flowers of different species of plants, the honeybees are supposed to make use of certain clues, such as the colour, form, scent, and the position of the flowers. However, it is only in the European honeybee *Apis mellifera* that these factors of sensory physiology and behaviour have been analysed and have been proved to be of importance in the phenomenon of flower constancy. It was with the object of investigating the possible importance of 'form' in the flower constancy shown by Indian honeybees that the present work was undertaken.

Considerable work on the problem of discrimination of form and pattern in *A. mellifera* based both on spontaneous preference and on preference induced by training has been done in Europe, especially by German workers.

Von Frisch (1914) trained honeybees to select a sunflower-shaped pattern from a gentian-shaped one, but neither he nor Hertz (1929a)

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[1] Dedicated to Prof. K. von Frisch on his seventieth birthday.

could succeed in training the bees to distinguish between such figures as triangles, squares, and circles. However, the bees could distinguish these patterns from the subdivided ones, and they could easily be trained to choose only the more subdivided pattern. Hertz (1929b) also performed experiments on the spontaneous, as opposed to induced, form-preference in *A. mellifera*. She did these by training bees to feed from a uniform white surface and then offering them a choice of two alternative black-on-white patterns on which they had never been fed. They preferred any black figure to the white background and so Hertz came to the conclusion that their spontaneous preference regarding various figures was related to the quantity of outline, irregularity and size of patterns, and the independence of their components. There was no absolute criterion of attractiveness, but the attractiveness of any pattern depended upon its value relative to that of other objects which the bee could see at that time. At any rate, bees preferred the most contrasting patterns. Later, Hertz also performed experiments with three dimensional models. The result was that bees responded to the shadows of these three dimensional models in the same way as they did to the black parts in the black-on-white patterns.

Gertrud Zerrahn (1933), who trained honeybees to one pattern and then presented them with a choice of two patterns which were similar in character but different in their degree of subdivision, also concluded that the bees had a spontaneous tendency to alight upon whatever pattern possessed the greatest length of contour. Wolf and Zerrahn-Wolf (1935) offered untrained honeybees a free choice of pairs of chessboard patterns and they concluded that the reaction of bees to patterns depended only on the rate of change in the stimulation of their eyes. Wolf (1933 a, b) demonstrated the importance of 'flicker' in bee vision, and concluded that the quick variation in the stimulation of the facets would cause the bee to alight, and discover groups of flowers.

This simple hypothesis, however, can not explain all the observed facts. After taking a review of all the work done on this subject, including her own work, Hertz (1935) concluded that the amount of outline possessed by different black-on-white patterns was certainly not the only quality by which they were distinguished; a figure was perceived as a complex thing, which might have several different properties which could be used for alternative training.

From the foregoing, it appears that our knowledge of the subject of form discrimination in honeybees is far from complete. The conclusions reached by Hertz, Wolf, and Zerrahn are partially contradictory. Ribband's book (1953) contains a wealth of information on the vision of honeybees and yet his section on 'Perception of Form and Pattern' leaves the impression that much more data are necessary. There is, however, a certain measure of agreement on one point, namely that, when the bees are confronted with a pair of figures of similar general character (but differing in the amount of contour or degree of subdivision), they prefer the figure with greater contour to the one with less, as long as they are able optically to resolve both patterns and consequently recognise them as such.

In attempting to investigate the response of the Indian honeybees to form and pattern, the following problems were posed:

(i) What preferences, if any, do the various species of Indian honeybees show for one of two patterns similar in all respects except in their length of contour (or degree of subdivision, contrast, degree of brokenness, etc.)?

(ii) If there is such a preference, is there a point of subdivision of pattern at which this preference is reversed? And if so, when?

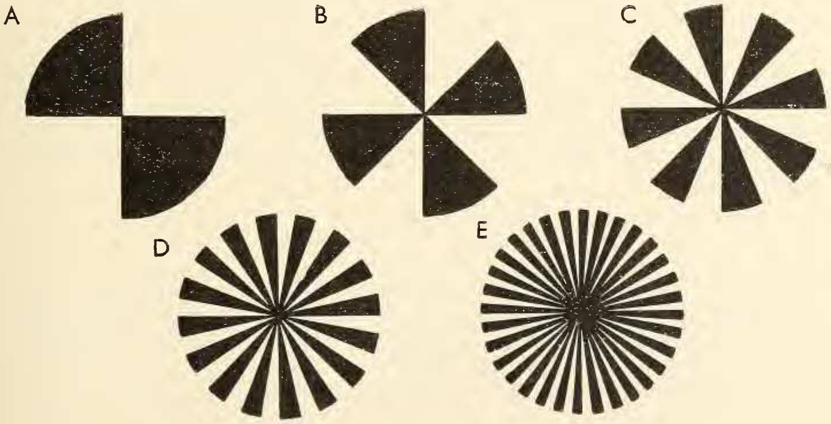
(iii) Does the choice of pattern depend on the distance at which the bee decides on which of the two to alight?

2. MATERIALS

Results recorded in this paper have been obtained from experiments on *Apis indica* and *Apis florea*. During the training of the bees and the tests, the experimental table was covered with a uniform light grey paper. During the test this background of light grey served to provide a strong contrast to all other patterns provided which were made in jet black.

Two series of patterns (or figures) similar to some used by Zerrahn (1933), one later referred to as the star series, and the other the chequerboard (or chessboard) series, have been used in these experiments. In the star series of patterns, photographic black paper was cut and stuck on light grey (same as the background colour) cardboard discs.

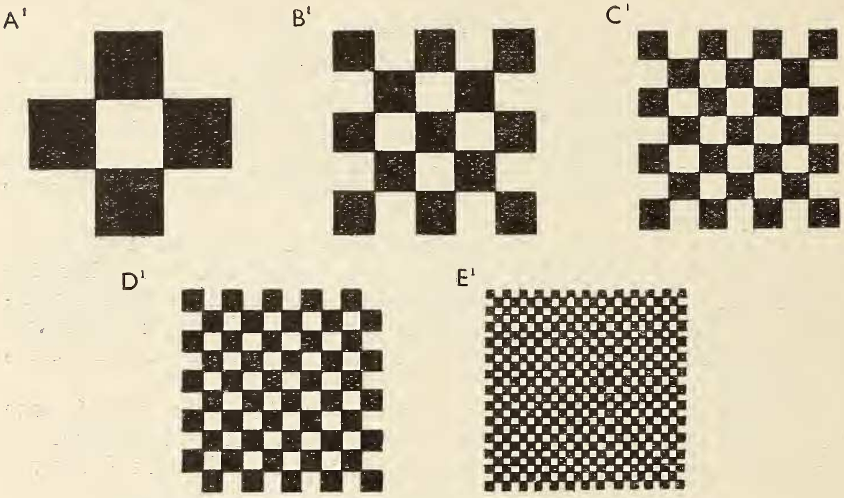
The radius of each pattern was always the same, namely one inch. The star series consisted of five gradations of patterns of increasing complexity shown in text figure 1 (A-E). Pattern A showed the least amount of contour between black and light grey. The amount of contour increases successively through B, C and D to reach its climax in E. Two specimens of each grade of pattern were prepared. In addition to these patterns, two specimens each of solid black discs and solid medium grey discs of the same diameter as the black rays



TEXT-FIGURE 1. Star series of patterns A to E.

in the star series were prepared. The medium grey chosen (M 15 of the standardized Baumann series) was approximately intermediate in shade between the light grey and the black used in these experiments.

In the chessboard series two figures each of five grades of patterns of increasing contour complexity were prepared. Here, however, the black parts of the figure were not stuck on light grey squares but were painted jet black in Indian ink on it. The five grades in the chessboard series are designated as A′, B′, C′, D′, and E′ (figure 2). The least subdivided pattern A′ presents the least amount of contour of black and light grey, while the degree of subdivision as well as the amount of contour increases successively through B′, C′ and D′ to reach its climax in E′. Two specimens of medium grey squares (M 15) were also prepared for the chequerboard series.



Text-figure 2. Chequerboard series of patterns A′ to E′

3. Method of Experiments

At the beginning of the experiments with each of the two species of honeybees the bees had first to be lured to the experimental table in order to perform the experiments. The method of luring both *A. indica* and *A. florea* is essentially the same. The bees are lured either directly from the hive when it is accessible, or else from the flowers on which they feed in nature. During luring a piece of filter paper smeared with honey is held near the bees. When one of the bees happens to crawl on this honey-soaked filter paper it feeds from it. After feeding, the bee returns to the hive and apparently alerts its companions, for in a short while a group of about ten to fifteen bees is seen feeding from the filter paper. The filter paper together with the bees thereon, is then slowly transferred, by stages, to the experimental table where concentrated sugarwater drops are uniformly scattered over a transparent piece of 'Perspex' (I.C.I.) which, in its turn lies above the light grey paper which forms the background colour. The filter paper together with the bees on it is finally kept near one of these sugarwater drops. When the honey on the filter paper is exhausted, bees discover the sugarwater drops and commence feeding on them. The filter paper is then discarded. Thereafter, the bees regularly visit the experimental table and feed on sugarwater drops. The sugarwater drops are renewed as soon as they are exhausted. This part of the experiment is called the training. The bees in this case are being trained to associate food with the light grey colour of the uniform background. If the bees have been fed for a sufficiently long time on a given spot, they automatically visit the same spot at approximately the same hour on subsequent days. This fact obviates the need of luring the bees to the experimental table every day.

The perspex, referred to above, is of the same appearance as glass but differs from it inasmuch as it does not cut away the ultra-violet rays to the same extent. During the training of the bees as well as the tests, a piece of perspex covers the whole arrangement, either of the light grey paper alone or with the patterns on it as the case may be. This is to ensure that the bees do not train themselves to the smell of the light grey paper.

During training the perspex, over which sugarwater drops are laid, is cleaned at frequent intervals by means of a moist cloth. This precaution is taken to ensure that the bees do not associate the bee scent with food. This has been shown to occur in *A. mellifera* and so is suspected to occur also in the Indian species of honeybees. Care is also taken during training to see that the bees do not form large clusters round a single sugarwater drop; for if this is allowed to happen the bees might get trained to an accumulation of their own shapes and colour, instead of to the light grey colour and this factor may distort the results to be obtained in the test.

After training to the light grey background, tests are performed with figures on which the bees had not been fed. In the test, two specimens each of two patterns for which the bees' inborn preference is to be tested are kept on the light grey paper which is already on the training table, and this whole arrangement is covered over by a new clean sheet of perspex. The patterns are laid out on the table in such a manner that all of them have an equal chance of being visited by the bees. In the tests, no sugarwater drops are offered over the perspex. Ordinary water drops were offered instead on the perspex directly above the patterns, in some of the tests, while in the rest there were no drops. The presence of water drops in the test merely serves to enhance the number of visits on all the patterns offered, but does not materially alter the nature of the results. In the tests where the perspex is raised, the presence of water drops greatly facilitates accurate recording of the number of visits, which is otherwise very difficult. The number of visits that the bees pay to each of the patterns offered is recorded. When a sufficient number of visits have been recorded the test is closed down, and training the bees to light grey paper is resumed in the manner described above.

During each test the experimental table is turned once through an angle of 90°, so as not to give any pattern (also called 'figure' in this paper) an advantage over the other only because of its position.

The reaction of bees to figures were tested under two main conditions:

(a) with the figures covered only with a layer of perspex, and

(b) with perspex raised over the figures so that it covered the whole arrangement at a distance of $1\frac{1}{2}''$. For this purpose a frame was designed which could be used to raise the perspex and which, at the same time, prevented the entry of the bees from below it.

4. OBSERVATIONS

The results obtained in the experiments with the two species of honeybees are recorded below in the form of tables. The signs in the column at the extreme right in the table show which pattern (the less subdivided or the more subdivided) out of a pair is preferred by the bees, and to what extent? The signs used to indicate the preferences are +, + +, and + + +. These are explained below Table 1. The preferences shown by the bees in these experiments are entirely spontaneous or inborn, inasmuch as the tests are not preceded by training the bees to any particular pattern. It is significant that the choice between the two patterns by the bees is based on relative and not on absolute characters of the patterns in question.

Table 1 and 2 show the results of experiments with *A. indica* in which the star and the chequerboard series of patterns respectively were used. Tables 3 and 4 record the results of experiments with *A. florea* in which also the star and the chequerboard series of pattern respectively were used.

TABLE 1

Apis indica. Star series of patterns

Expt. No.	Patterns offered	Perspex raised or not ?	Percentage of visits on each of the patterns	Total No. of visits	Remarks*	
					Less sub.	More sub.
1	A & B	No	A – 33·3, B – 66·7	42		+ +
2	B & C	No	B – 33·3, C – 66·7	120		+ +
3	C & D	No	C – 50 , D – 50	32	equal	equal
4	C & D	Yes	C – 71·4, D – 28·6	49	+ +	
5	D & E	No	D – 54·2, E – 45·8	35	+	
6	Black disc & E	No	Black 13·6, E – 86·4	44		+ + +
7	B & E	No	B – 33·3, E – 66·7	37		+ +
8	B & E	Yes	B – 71·4, E – 28·6	63	+ +	
9	A & E	No	A – 32·5, E – 67·5	40		+ +
10	A & C	No	A – 25, C – 75	32		+ + +
11	A & C	Yes	A – 67·5, E – 32·5	40	+ +	
12	M15 & E	No	M15 – 15·3, E – 84·7	13		+ + +
13	M15 & E	Yes	M15 – 52, E – 48	48	+	
14	M15 & D	Yes	M15 – 46·2, D – 53·8	54		+

* Slightly preferred +, preferred + +, greatly preferred + + +.

TABLE 2

Apis indica. Chequerboard series

Expt. No.	Patterns offered	Perspex raised or not ?	Percentage of visits on each of the patterns	Total No. of visits	Remarks	
					Less sub.	More sub.
1	B′ & E′	No	B′ – 75·5, E′ – 24·5	49	+ + +	
2	Black sq. & C	No	Black – 20, C′ – 80	35		+ + +
3	B′ & D′	No	B′46·6, D – 53·4	30		+
4	B′ & D′	Yes	B′ – 67, D′ – 33	59	+ +	
5	D′ & E′	No	D′ – 81, E′ – 19	37	+ + +	
6	Black sq. & E	No	Black – 29·6, E′ – 70·4	27		+ +
7	M15 & D′	Yes	M15 – 63·1, D′ – 36·9	38	+ +	

TABLE 3

Apis florea. Star series of patterns

Expt. No.	Patterns offered	Perspex raised or not ?	Percentage of visits on each pattern	Total No. of visits	Remarks	
					Less sub.	More sub.
1	A & B	No	A – 34·7, B – 65·3	46		+ +
2	A & B	Yes	A – 45·9, B – 54·1	49		+
3	A & C	No	A – 23·8, C – 76·2	88		+ + +
4	A & C	Yes	A – 38·9, C – 61·1	77		+
5	A & D	No	A – 26·8, D – 73·2	97		+ +
6	A & D	Yes	A – 50·5, D – 49·5	175	equal	equal
7	A & E	No	A – 24·3, E – 75·7	111		+ + +
8	A & E	Yes	A – 47·1, E – 52·9	89		+
9	B & E	No	B – 39.4, E – 60·6	152		+
10	C & D	No	C – 55·3, D – 44·7	94	+	
11	D & E	No	D – 52, E – 48	104	+	
12	M15 & D	Yes	M15 – 49·7, D – 50·3	119	equal	equal

TABLE 4

Apis florea. Chequerboard series

Expt. No.	Patterns offered	Perspex raised or not ?	Percentage of visits on each pattern	Total No. of visits	Remarks	
					Less sub.	More sub.
1	A′ & B′	No	A′ – 42·6, B′·57·4	54		+
2	A′ & C′	No	A′ – 24·3, C′ – 75·7	82		+ +
3	A′ & D′	No	A′ – 27·3, D′7·27	117		+ +
4	A′ & D′	Yes	A′ – 46·4, D′·53·6	114		+
5	A′ & E′	No	A′ – 48·7, E′ – 51·3	78		+
6	D′ & E′	No	D′ – 55·5, E′ – 44·5	63	+	
7	D′ & E′	Yes	D′ – 55, E′ – 45	69	+	
8	M15 & D′	Yes	M15 – 48, D′ – 52	98		+

5. DISCUSSION

One of the most significant and interesting results obtained from the present study was that both the species of honeybees, even when they were trained to feed only from a uniform light grey surface, visited in overwhelmingly large numbers the black-on-light grey patterns offered to them in the test, whereas the grey background to which the bees had been trained attracted only very few.

In *A. indica* it is seen (Table 1) that among pairs of star patterns which differ but little from each other as regards the amount of contour (or the degree of subdivision) they present, the more subdivided figure is nearly always preferred (though sometimes only slightly) to the less subdivided one, as seen in Experiments 1 and 2, or at least the less subdivided figure is never preferred to the more subdivided one (e.g., Expt. 3). If the difference in the amount of subdivision is greater between the two figures, as in Expt. 10, the more subdivided pattern is markedly preferred to the less subdivided one.

If this inference is correct, then it is to be expected that the preference of the subdivided figure will cease (or even be reversed) as soon as the limit of the optical resolution of the pattern in question, by the eyes of the bee is reached. This supposition, in fact, seems to be correct in the case of *A. indica*. The results of Expt. 5 show clearly that a point is reached when the less subdivided figure (D) (text figure 1) is preferred to a more subdivided one (E). Thus, at the level of subdivision as exemplified by E, the limit of optical resolution for *A. indica* is reached.

Though we find in the abovementioned case that the less subdivided figure is slightly preferred to the more subdivided one, yet the difference in the percentage of visits between the two is small; that is to say, there is no sudden reversion of preference. This might be explained by the assumption (confirmed by direct observation) that the distance at which each bee discriminates between the two patterns is not constant, but varies round a certain median value, most probably according to a Gaussian curve. Consequently, for a certain number of bees which decide at a greater distance, the finer pattern will have become already blurred while other bees, flying low, still recognize and therefore prefer it.

If this interpretation is correct then the preference for the less subdivided figure should visibly increase if the bee is forced to make her choice between the two at a greater distance. This has been effected by the abovementioned device of raising the perspex so that the distance between it and the plane of the figures becomes $1\frac{1}{2}''$. In this case, $1\frac{1}{2}''$ is the minimum distance from which each bee can view both the patterns and choose between them. In fact, in Expt. 4 (Table 1) where this has been done the less subdivided figure C is definitely preferred to the more subdivided one D. This result is substantially different from the result obtained in Expt. 3, where the same patterns were used but without raising the perspex. The same phenomenon is even more strikingly illustrated by Expts. 7 and 8, as also by Expts. 10 and 11. In all these cases, the bees behave as if for all or most of them the more subdivided patterns E, D and even C become blurred when viewed from a distance of 1½″. We assume that such blurred star figures of black-on-light grey appear rather like medium grey discs to the bee. The fact that the finely divided star pattern D when confronted with a medium grey disc (M 15) under a raised perspex is almost exactly as attractive to the bees as the latter (Expt. 14) fits in with this assumption. The same holds for the star pattern E (Expt. 13). It is obvious that when the perspex is not raised above the plane of the figures, a greater proportion of bees will always be able to distinguish and prefer the finer pattern, hence even the border line pattern E is preferred to B (Expt. 7) and to A (Expt. 9). However, the preference of E is not quite commensurate with its degree of subdivision.

The results obtained, when the chequerboard series of patterns are offered to *A. indica* in pairs (Table 2), are in conformity with the results obtained with the star series and thus substantiate the hypothesis of the form discrimination of *A. indi*ca outlined above. The limit of optical resolution is reached for the bees at E′ (text figure 2) of the chequerboard series, as shown by Expt. 5. The only puzzling result is that of Expt. 7. Here the compact figure M 15 not only reaches the attractiveness of the finely subdivided figure D′ but surpasses it when the perspex is raised. This is contrary to the assumption that the visits on this could never more that equal those on D′, even if the chequerboard becomes completely blurred and therefore similar to a grey square of the same luminosity.

Results of a similar nature are obtained with *A. florea*. Results of Expts. 1, 3, 5, 7 and 9 in Table 3 illustrate the fact that the untrained bees when confronted with pairs of star patterns always prefer the more subdivided patterns to the less subdivided ones. These results are quite comparable to those obtained with *A. indica*. That, from a certain degree of subdivision of pattern, the preference of the bees is reversed in favour of the less subdivided figure is shown in *A. florea* by the result of Expt. 10. Here the less subdivided figure C is preferred (though slightly) to the more subdivided figure D. Thus it seems that for a certain amount of bees the limit of optical resolution of patterns is almost reached in *A. florea* between C and D of the star series of patterns. This is in contradistinction to the case obtained in *A. indica* where, as shown by Expt. 3 of Table 1, the limit of resolution is not quite reached between C and D. The fact that in *A. florea* the bees already prefer figure C to figure D seems to indicate that they have a lower visual acuity as compared with *A. indica.*

The result of Expt. 11 under Table 3 corresponds with the result of Expt. 5 in Table 1, thus showing that for both *A. florea* and *A. indica* the finely subdivided pattern E has less attraction than the less subdivided pattern D. Results of Expts. 2, 6 and 8 in Table 3 show that, as in *A. indica,* the preference is reversed in favour of the less subdivided pattern in *A. florea* when the perspex is raised 1½″ above the plane of the figures offered. The only result which does not fit in is that of Expt. 4 in Table 3. For this experiment seems to show that *A. florea* still prefers pattern C to pattern A, even when the perspex is raised by 1½″. This result differs from the result of Expt. 11 in Table 1 where under similar conditions *A. indica* showed a definite preference for pattern A over pattern C. Expt. 12 in Table C shows that for *A. florea* pattern D is very much similar to a medium grey disc when the perspex is raised to a height of 1½″ above the figures in the test. This result agrees with the result obtained with *A. indica*.

Table 4 contains the results of experiments on *A. florea* in which the chequerboard series of pattern were used. In experiments 1, 2 and 3 the patterns displaying greater contour are preferred to those showing less. Expt. 5 shows that the most subdivided pattern of the series, E′, is slightly preferred to the least subdivided one, namely A′. Unfortunately the same experiment was not performed for *A. indica* but a closely comparable experiment, Expt. 1 in Table 2, shows that the most subdivided pattern E′ is not preferred to one of the less subdivided patterns B′. In fact B′ is nearly thrice as much visited as E′. This fact seems to indicate that *A. florea* has a greater visual acuity than *A. indica*. But this is contradictory to the previous hypothesis. Also Expt. 8 shows that, unlike *A. indica*, the medium grey M 15 is confused with pattern D′ when the perspex is raised in the test to a height of 1½″. Other results in Table 4 are similar to those obtained with *A. indica*.

Thus, as in the case of *A. mellifera,* a figure or pattern which presents a greater contour is preferred to one with less both by *A. indica* and *A. florea*. This preference, however, is shown only as long as the eye of the bee is able to resolve a pattern as such. Beyond that limit the preference of the more subdivided figure is reversed, most probably because such a figure seems blurred to the bees. In my experiments the reversal which occurred when the distance between the contours reached a certain absolute value was not sudden but gradual. This points to the fact, confirmed by observation, that the distance at which the bees make their choice between alternative patterns is not the same for all of them, but there is a median value around which the other values of distance lie, most probably along a Gaussian curve. It is intended, in future work, to obtain comparative values of visual acuity for the different species of honeybees by introducing an arrangement whereby the bees would be compelled to make their choice between different patterns at certain constant distances. The results obtained are likely to lead to a more definite conclusion than is possible on the basis of the present work, purely from the point of view of difference, if any, in the visual acuities of the different species of bees. The results thus far obtained seem to suggest that *A. florea* might have a slightly greater visual acuity than *A. indica*.

6. SUMMARY

As in the case of the European honeybee, *A. mellifera,* a pattern which presents a greater contour is spontaneously preferred to one with less, both by *A. indica* and *A. florea*. This preference is shown only as long as the bee's eye is able to resolve a pattern as such. Beyond that limit the preference of the more subdivided figure is reversed, most probably because such figure seems blurred to the bees. This reversal is not sudden, but gradual. This points to the fact that the distance at which the bees make their choice between alternative

patterns varies for different species of bees around a median value, most probably along a Gaussian curve. The results thus far obtained seem to suggest that *A. florea* may have a slightly greater visual acuity than *A. indica.*

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